Habitat width along a latitudinal gradient

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   Abstract:
We use the Chowdhury ecosystem model, one of the most complex agent-based ecological models, to test the latitude-niche breadth hypothesis, with regard to habitat width, i.e., whether tropical species generally have narrower habitats than high latitude ones. Application of the model has given realistic results in previous studies on latitudinal gradients in species diversity and Rapoport's rule. Here we show that tropical species with sufficient vagility and time to spread into adjacent habitats, tend to have wider habitats than high latitude ones, contradicting the latitude-niche breadth hypothesis.

   Keywords:
Chowdhury ecosystem model, latitude-niche breadth hypothesis, Rapoport's rule, latitudinal gradients in species diversity, vagility, species-area relationship, fractal dimensions.

1   Introduction

According to a widely held view, an increase in diversity must result in a narrowing of niches, in denser species packing. Thus, according to Rosenzweig & Ziv (1999) "Theory suggests that higher diversity should shrink niches, allowing the coexistence of more species". Applied to latitudinal gradients, the much greater species richness in the tropics than in colder environments is thought possible only because species are more densely packed, i.e., have smaller niches. This view (the so called latitude-niche breadth hypothesis) can be traced back to MacArthur (MacArthur 1965, 1969, 1972; MacArthur & Wilson 1967), but is probably even older. There is some empirical evidence for this view (e.g., MacArthur 1965, 1969; Moore 1972), and much against it (e.g., Rohde 1980; Novotny & Basset 2005). For example, concerning one aspect of the niche, the latitudinal range of a species, some studies have provided support for the view that latitudinal ranges are narrower at low latitudes (Rapoport's rule, e.g. Stevens 1989), whereas others have found no support or evidence for an opposite trend (e.g., Rohde et al. 1993). Rohde (1998) therefore suggested two opposing trends: newly evolved species with

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little vagility may have narrower ranges in the tropics, species with greater vagility and of sufficient age to spread into adjacent areas may have larger ranges. The same may apply to habitat width and niche width in general.

In this paper, we use the Chowdhury ecosystem model (Chowdhury & Stauffer, 2005; Stauffer et al. 2005) to examine the latitude-niche breadth hypothesis with regard to one of the most important niche dimensions, the habitat width. We check the effect of vagility and age of ecosystem on habitat width. We have applied the model before (Rohde & Stauffer 2005; Stauffer & Rohde 2006) to study the variation of species diversity and latitudinal ranges with latitude, comparing cold with tropical regions in simulations of the whole range of latitudes in a lattice model, and got realistic results.

2   Methods

The Chowdhury model (Chowdhury & Stauffer, 2005; Stauffer et al. 2005) is one of the most complex agent-based (Billari et al. 2006) ecological models (Pękalski, 2004; rimm & Railsback, 2005) and has been reviewed e.g. in Stauffer et al. (2006). Each species may move to a neighbouring lattice site where it is still the same species. Further details are given in an appendix.

One open question is the fractal dimension D of the number N of species found in a square of side length L:

$$N \propto L^D.$$

Empirically, fractal dimensions $1.2 \leq D \leq 2.3$ are given by Rosenzweig (1995), whereas $D = 2$ would correspond to a trivial proportionality of the number of species and the area in which they are counted. The rationale behind our comparison of fractal dimensions is: in the extreme case, the largest square could have a single species, which is also found in the smallest square, i.e., the slope is 0, the species' habitat is very wide. On the other hand, the largest square could have 100 species, 10 of which are also found in the smallest square, i.e. the slope is much steeper, the habitats are much narrower.

An earlier attempt (Stauffer and Pękalski (2005) roughly gave this simple proportionality when it used the low vagility d (diffusivity) which gave good results in Rohde & Stauffer (2005) and Stauffer & Rohde (2006). However, while in these papers we simulated the whole Earth from the north pole to the south pole, tests of the above exponent D should look at smaller,

more homogenous regions. Thus, the vagility d, which is the probability that a species invades a neighbouring lattice site during one time step, has to be larger for smaller lengths associated with the neighbor distance. Thus we now use larger d than in Stauffer & Pękalski (2005), Rohde & Stauffer (2005) and Stauffer & Rohde (2006) and also systematically vary the observation time (measured in Monte Carlo steps per site; we refrain from identifying it with years). We simulate (in most cases) ten $L \times L$ square lattices, with the other parameters besides vagility and observation time as in Rohde & Stauffer (2005) and Stauffer & Rohde (2006). Each such simulation either refers to tropical or to high latitude (here referred to as polar) regions. As in Rohde & Stauffer (2005) and Stauffer & Rohde (2006), we use the standard Chowdhury model for the simulation of the tropical region, while for the polar region the birth rate is reduced by a factor 4. This birth rate is the probability per iteration that offspring reaching maturity is being produced, due to the harsh living conditions in polar regions we assume this probability to be four times lower than in the tropics.

3   Results

Fig.1 sums up the species number N over all lattice sites and over all time steps after equilibration. The headlines give the observation times varying from two thousand to two million time steps, for various lattice sizes.

We see that for short times the species barely had a chance to move much from their site of origin, and thus N is roughly proportional to the area: $D = 2$. The longer the observation time is, the more could the species spread over the lattice, and the smaller is the slope of our log-log plots. It appears that the slope is smaller in the tropics, which means that habitats are not narrower but somewhat larger there than in polar regions, if they had sufficient time to spread.

Fig.2 shows for a fixed observation time of 200,000 that the slope D becomes the larger the smaller the vagility is, thus explaining the results of Stauffer and Pękalski (2005). For the smallest $d = 0.001$ the data follow nearly perfectly a line with slope $D = 2$, for the largest $d = 0.1$ the curves starts with $D = 1$. For small d one no longer sees the difference in the polar and tropical slopes which is seen for large d.

All these slopes D agree with reality (Rosenzweig 1995) but do not come from good straight lines; our log-log plots in general show upward curvature,
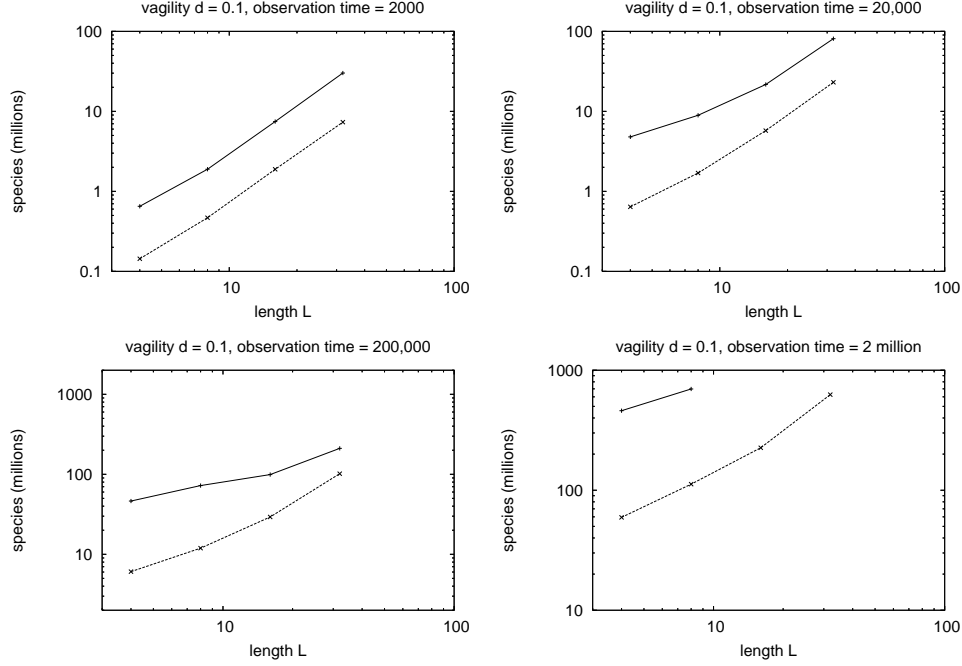
Figure 1: Variation of the number N of species with the length L of the square, $L = 4$, 8, 16 and 32. The vagility is $d = 0.1$ for all four cases. Upper lines = tropics, lower lines = polar.

and the slopes are those for intermediate lattice sizes. Asymptotically for longer times and much larger lattice sizes L we expect the trivial proportionality with $D = 2$ since then the range ℓ over which a species is spread obeys $1 \ll \ell \ll L$. The real Earth, however, may not correpond to these mathematical limits but to finite sizes L at finite times.

Fig.3 shows that the results are not merely a function of the product of vagility and observation time; varying d influences many other properties (Rohde and Stauffer 2005) and not only the time scale.

4   Discussion

The findings presented in Fig. 1 contradict the latitude-niche width hypothesis, for the niche dimension "habitat width", according to which habitats are narrower in the tropics. Indeed, they provide evidence for an opposite
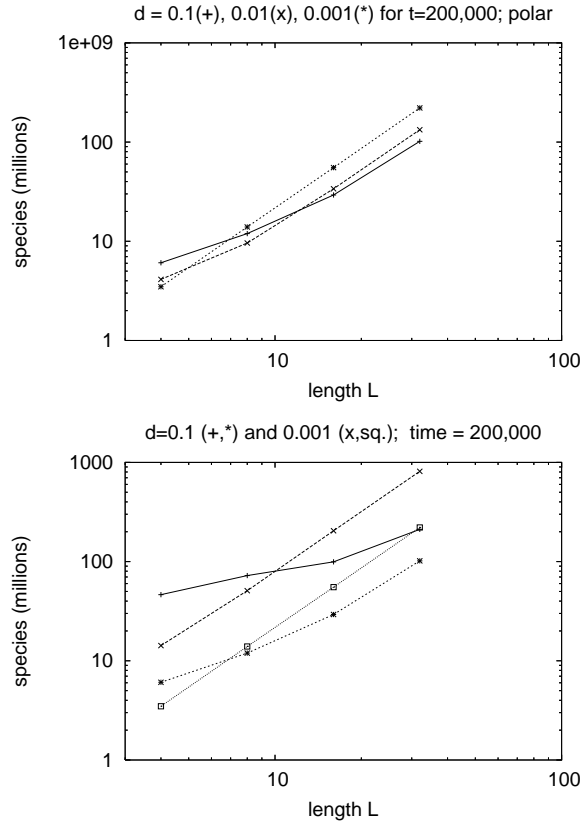
Figure 2: Variation of N versus L for various d at fixed observation time of 0.2 million. Upper part: polar; lower part: x and + for tropics, stars and squares for polar.

effect: habitats are even larger near the equator than at high latitudes. This agrees with the findings of Stauffer & Rohde (2006) who did not only fail to find support for Rapoport's rule, but showed that latitudinal ranges are wider in the tropics, in agreement with much empirical evidence.

The findings presented in Fig. 2 show that habitats are smaller in species with little vagility, in accordance with the hypothesis, developed in the context of Rapoport's rule, that young species (or subspecies) with little vagility, which have not had sufficient time to spread into wider areas, have narrower latitudinal ranges at low latitudes (Rohde 1998).

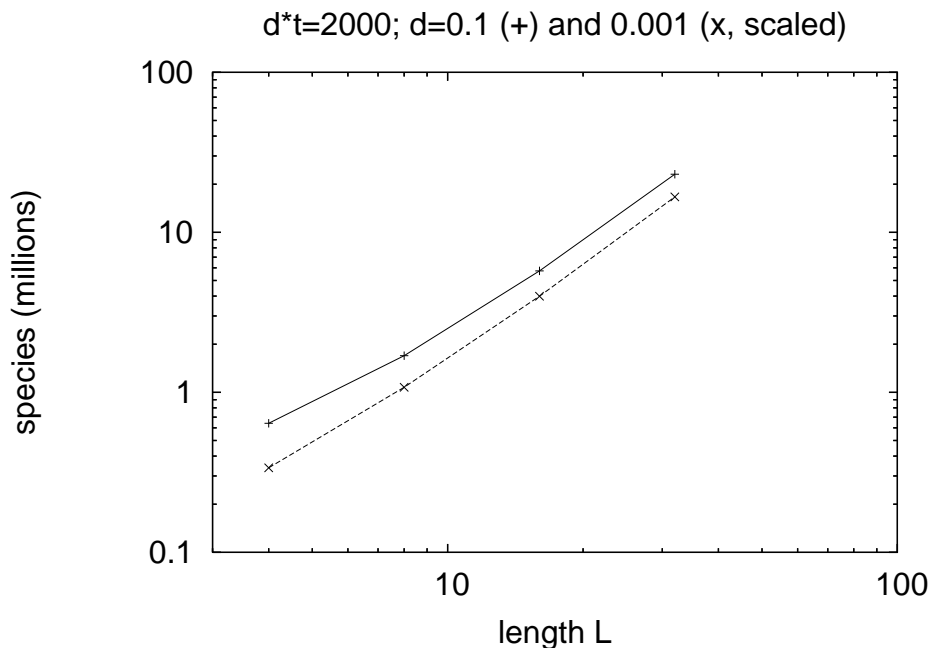Empirical evidence for the latitude-niche breadth hypothesis is ambigu-

Figure 3: Variation of polar N versus L for two vagilities d and two observation times t such that dt is constant.

ous. For example, Moore (1972) found that the average tropical species occupies about half as much of the intertidal zone as the average temperate species. According to MacArthur (1965, 1969), tropical species often have a spottier distribution than high-latitude ones. Concerning one aspect of the habitat of animals and plants, i.e. their latitudinal ranges, Stevens (1989) provided evidence that some plant and animal species have narrower latitudinal ranges in the tropics, referring to this phenomenon as Rapoport's rule. Some of the numerous subsequent studies also provided evidence for the rule (review in Rohde 1999).

However, support for the existence of narrower habitats in the tropics is far from unequivocal. The studies that did not find support for Rapoport's rule are more numerous than those that did, and in those cases in which species have larger latitudinal ranges at high latitudes, the increase is often restricted to high latitudes above approximately 40-50 ^{o} N and S (review in Rohde 1999). Rohde (1996) therefore suggested that the rule describes a

local phenomenon, the result of the extinction of species with narrow ranges during the ice ages.

1) Several authors (e.g. Beaver 1979; review in Novotny & Basset 2005) have studied possible differences in host specificity of herbivorous insects in tropical and temperate climates. No major differences were found. 2) Detailed studies deal with latitudinal gradients in habitat width of parasites of marine fish. Rohde (1978) has shown that host ranges (the number of host species infected) of ectoparasitic Monogenea infecting the gills are more or less the same at all latitudes, whereas host ranges of another group of (endoparasitic) flatworms, the Digenea, are markedly greater at high latitudes. However, when correction was made for intensity and prevalence of infection, host specificity was the same and very high at all latitudes for both groups (Rohde 1980). Other niche dimensions of these parasites, such as geographical range and microhabitat width, were also examined and found not to be correlated with diversity, although the data sets were small and more studies are needed. Host size may on average be smaller in the tropics, due to the very large number of host species, many of them small (Rohde 1989). 3) Lappalainen and Soininen (2006) analysed the determinants of fish distribution and the variability in species' habitat breadth and position along latitudinal gradient of boreal lakes and found that the regional occupancy of species was more strongly governed by the habitat position than the habitat breadth. The cool water species (percids and cyprinids) showed significant decrease in habitat breadth towards higher latitudes (and not towards lower latitudes, expected by the latitude-niche breadth hypothesis). 4) Some further examples are discussed in Vázquez & Stevens (2004).

Vázquez & Stevens (2004) have reviewed the evidence for the latitude-niche breadth hypothesis, using meta-analytical techniques. They found that the results of the meta-analysis do not permit rejection of the null hypothesis of there being no correlation between latitude and niche breadth. They also critically examined the two assumptions on which MacArthur's hypothesis are based, i.e., 1) that there is a latitudinal gradient in population variability, and 2) that there is a relationship between population variability and niche breadth. These assumptions are widely accepted (e.g., May 1973). They claim that the tropics have greater stability and less seasonality than temperate regions, making populations more stable, thus allowing narrower niches. However, Rohde (1992) has pointed out that there may be extreme variations in temperature, salinity and currents in tropical shallow waters, such as high diversity coral reefs. Such variations may occur over short

time spans of a few hours. The meta-analysis of Vázquez & Stevens (2004) shows that available evidence does not support the view of an increasing population variability with latitude, and evidence for narrower niches of less variable populations is at best equivocal and does not permit rejection of the null hypothesis of no relationship.

In spite of these criticisms of the mechanism involved, there could be a latitudinal gradient in niche width due to other mechanisms. Vázquez & Stevens (2004) suggest such a mechanism. Greater specialization may be a by-product of the latitudinal gradient in species diversity, because nestedness leads to an asymmetric, i.e. faster increase of specialized species than of communities. In other words, nestedness and asymmetric spezialisation tend to increase with the number of species in a network. Vázquez & Stevens (2004) pay particular attention to parasites. Nestedness of interactions between species has, for example, been observed in marine Monogenea (Morand et al. 2002), for which group, however, host specificity does not change with latitude. Overall, nestedness is not common among parasites of fish (Rohde et al. 1998; Poulin & Valtonen 2001).

Finally and importantly, the latitude-niche breadth hypothesis as formulated by MacArthur and his followers makes equilibrium assumptions, and it implicitly and explicitly assumes that habitat space is more or less filled with species. However, there is much evidence that there is an overabundance of vacant habitats and that most ecological systems are far from saturation (for a discussion and examples see Rohde 2005). This removes the very basis on which the hypothesis rests. The Chowdhury model does not make equilibrium assumptions and incorporates vacant niches. Our simulations using this model are further evidence against the latitude-niche breadth hypothesis: tropical vagile species that have had sufficient time to spread away from their original habitat, do not have narrower but wider habitats than high latitude species.

How can we reconcile our results, that habitats of species are somewhat larger in the tropics than at higher latitudes, with the well known latitudinal gradient in species diversity? One possible explanation is the idea of Terborgh (1973) and Rosenzweig (1995), that tropical zones are generally larger and therefore stimulate speciation and inhibit extinction. That larger areas (all other conditions being equal or at least similar) often accommodate more species, is well established. For example, at the level of geographical area, Blackburn and Gaston (1997) found that there is indeed a relationship between the land area and species richness of a region once tropical species are

excluded. This relationship is independent of the latitude and productivity of regions. A study on South American mammals (Ruggiero 1999) confirmed this: The number of principally extra-tropical mammal species per unit area depends on the biome area (for further examples see Rosenzweig 1995). However, as pointed out by Rohde (1998), although area matters, it cannot be the primary cause of the latitudinal diversity gradients: many high diversity tropical areas are much smaller than low diversity areas at high latitudes. Many recent studies have provided support for this view (e.g., MacPherson 2002: area size does not explain the latitudinal pattern in benthic species richness on a large spatial scale. Willig & Bloch 2006: "area does not drive the latitudinal gradient of bat species richness in the New World. In fact, area represents a source of noise rather than a dominant signal at the focal scale of biome types and provinces in the Western Hemisphere"). - Our results, that the habitats occupied by species are somewhat larger in the tropics than at higher latitudes, mean, with regard to latitudinal gradients, that there must be much overlap between habitats, leading to a far greater diversity in tropical than in high latitude areas of the same size. The larger (compared with high latitude) tropical areas (in Africa and the IndoPacific) would aggravate this. The overlap postulated here resembles the "Rapoport rescue effect" of Stevens (1989), according to which tropical species frequently "spill out" from their preferred habitat into adjacent less favourable ones, thus explaining the high diversity there. However, it is not necessary to distinguish favourable and less favourable habitats: species may simply "spill out" from the habitat where they have originated, into adjacent habitats that are as suitable.

5   Appendix: Model details

The Chowdhury model of ecosystem has been described and modified in many publications since 2003, and we give here only a short outline. Individuals are born, mature, produce offspring asexually, and die with a probability increasing exponentially with age after maturity. At most 100 animals fit into one habitat. Six trophic levels define pre-predator relations: The upper levels feed on the adjacent lower ones. The topmost level has one habitat, the second two, then 4, 8, ... At each iteration, with one percent probability the food habits, minimum age of reproduction, and number of births per iteration mutate randomly, allowing self-organisation of these parameters

through selection of the fittest. Death may come from from being eaten by a predator, from starvation, or from old age (with a high lifespan on the top food levels and a low lifespan on the bottom levels). If a species becomes extinct, then with probability 0.0001 per iteration the empty habitat is filled by another species. Each of the L^2 lattice sites carries such an ecosystem, each with dozens of living species. At the beginning, each different species gets a different number as its name. The number of differents species first decays with time (=iterations) and then fluctuates about some low average value.

Then with probability d at each iterations a species can migrate into a randomly selected neighbour site, if the corresponding habitat on that neighbour site is empty at that time. A random fraction of the population moves, the rest stays at the old site. Both parts of the population carry the same name, and in this way are counted as only once species spreading over more than one site. Summing up over all different surviving names we obtain the number of different species at that moment.

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